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Full Length Article

Distinct neural control of intrinsic and extrinsic muscles of the hand during single finger pressing

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ABSTRACT

Single finger force tasks lead to unintended activation of the non-instructed fingers, commonly referred to as enslaving. Both neural and mechanical factors have been associated with this absence of finger individuality. This study investigates the amplitude modulation of both intrinsic and extrinsic finger muscles during single finger isometric force tasks. Twelve participants performed single finger flexion presses at 20% of maximum voluntary contraction, while simultaneously the electromyographic activity of several intrinsic and extrinsic muscles associated with all four fingers was recorded using 8 electrode pairs in the hand and two 30-electrode grids on the lower arm. The forces exerted by each of the fingers, in both flexion and extension direction, were recorded with individual force sensors. This study shows distinct activation patterns in intrinsic and extrinsic hand muscles. Intrinsic muscles exhibited individuation, where the agonistic and antagonistic muscles associated with the instructed fingers showed the highest activation. This activation in both agonistic and antagonistic muscles appears to facilitate finger stabilisation during the isometric force task. Extrinsic muscles show an activation independent from instructed finger in both agonistic and antagonistic muscles, which appears to be associated with stabilisation of the wrist, with an additional finger-dependent modulation only present in the agonistic extrinsic muscles. These results indicate distinct muscle patterns in intrinsic and extrinsic hand muscles during single finger isometric force pressing. We conclude that the finger specific activation of intrinsic muscles is not sufficient to fully counteract enslaving caused by the broad activation of the extrinsic muscles.

1. Introduction

The human hand is capable of intricate individual finger movement patterns as playing the piano or typing, while most common movements – like grasping – involve simultaneous use of multiple fingers. The analysis of both types of movement show that fingers do not move independently from one another (Fish & Soechting, 1992; Häger-Ross & Schieber, 2000; Ingram, Körding, Howard, & Wolpert, 2008; Kaplan, 1965; Kim, Shim, Zatsiorsky, & Latash, 2008; Sanei & Keir, 2013; Soechting & Flanders, 1997). A recent study showed that this lack of individuation only starts after an initial range of movement in which independent movement is possible (Van Den Noort et al., 2016). Previous studies on force enslaving, i.e. the involuntary force production by non-intended fingers, investigated the factors limiting this independence (Kim et al., 2008; Van Duinen & Gandevia, 2011; Zatsiorsky, Li, & Latash, 1998).

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Both neural and mechanical constraints limit finger independence, and while these constraints may simplify the control of certain common multi-finger movements, they also enforce limitations on single finger mobility (Schieber & Santello, 2004; Soechting & Flanders, 1997; Zatsiorsky, Li, & Latash, 2000; Zatsiorsky et al., 1998). Another corroborated finding is that the highest indices of unintended movement can be found in the non-instructed fingers adjacent to the instructed ones (Kilbreath, Gorman, Raymond, & Gandevia, 2002; Kim et al., 2008; Schieber, 1991; Slobounov, Johnston, Chiang, & Ray, 2002; Van Beek, Stegeman, van den Noort, Veeger, & Maas, 2016; Van Den Noort et al., 2016; Zatsiorsky et al., 2000).

When considering both the neural and the mechanical constraints to the independence of finger movements, mainly the extrinsic hand muscles have been considered (Kaplan, 1965; Kilbreath et al., 2002; Sanei & Keir, 2013; Slobounov et al., 2002). However, the intrinsic muscles, located within the hand, are largely involved when it comes to the fine control of single finger movements. When performing different types of hand movements, the intrinsic and extrinsic muscles have distinct tasks. In a precision grip, all muscles are co-activated, and the muscle activity will increase with force (Adewuyi, Hargrove, & Kuiken, 2016; Maier & Hepp-Reymond, 1995). But while intrinsic muscles show high correlations to grip force, the extrinsic muscles have lower correlations (Milner & Dhaliwal, 2002; Winges, Kornatz, & Santello, 2008). More specifically, the intrinsic hand muscles have been indicated to control individuated and subtle manipulations of finger movements (Adewuyi et al., 2016; Milner & Dhaliwal, 2002; Winges et al., 2008). The lumbricals, at the palmar side of the hand, are not only involved in the flexion of the metacarpophalangeal (MCP) joints, but also in the extension of proximal interphalangeal (PIP) and distal interphalangeal (DIP) joints (Valero-Cuevas, 2005; Valero-Cuevas, Zajac, & Burgar, 1998). The agonistic and antagonistic extrinsic hand muscles together appear to be mainly used to stiffen the wrist and finger joints and play a role in providing the main force for the movement (Johnston, Bobich, & Santello, 2010; Li, Zatsiorsky, & Latash, 2000, 2001; Milner & Dhaliwal, 2002).

This study aims to investigate (1) the neural control of both intrinsic and extrinsic muscles during single finger presses, and (2) how this relates to finger force enslaving. To focus on the neural drive, received by both muscle groups, this study uses static finger presses as the influence of mechanical connections within the hand appears to be small in such conditions (Zatsiorsky et al., 1998, 2000). We test the following hypothesises: (1) Both intrinsic and extrinsic muscles will show co-activation of agonistic and antagonistic muscles in order to stabilize the finger and wrist; (2) In the intrinsic muscles, we expect to see modulation of this co-activation based on the instructed finger; (3) In the extrinsic muscles, we expect to see a more broad activation in both agonistic and antagonistic muscles, independently of the instructed finger, required for wrist stabilization.

2. Methods

2.1. Subjects

The study was approved by the local ethical committee (CMO Regio Arnhem-Nijmegen, The Netherlands), and written informed consent was obtained from all subjects. Thirteen healthy volunteers were included in the study, of which one was excluded from the analysis due to technical difficulties with the electromyography (EMG) recordings. Thus, the analysis was performed on 12 participants (age 25 ± 3 years, 5 men and 7 women).

2.2. Experimental setup

The index, middle, ring, and little finger of the right hand were taped to 4 individual force sensors (Micro Load Cell CZL635, Phidgets Inc, Calgary, Canada). The placement of the force sensors was adjusted both in the direction of the length and width of the

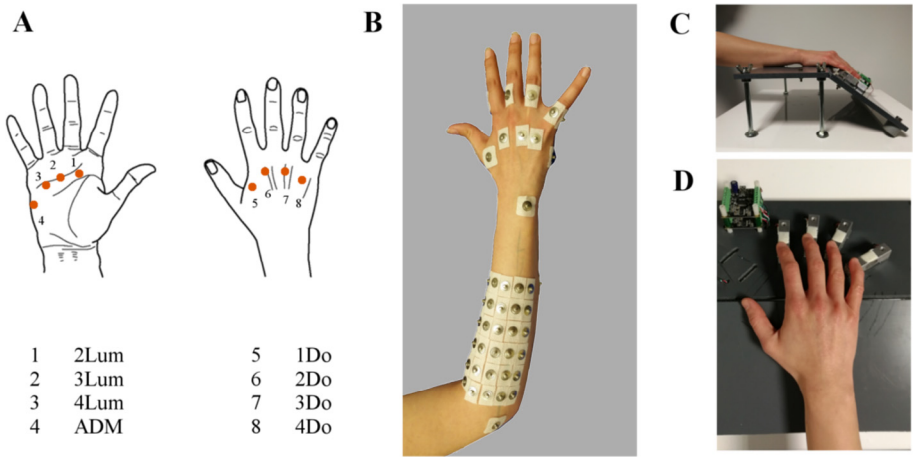

Fig. 1. (A) Position of intrinsic EMG electrodes. (B) View of placement electrodes on posterior side of the hand and arm. (C) Side view of custom force device. (D) Top view of custom force device. To insure clarity of the force device, pictures in (C) and (D) were taken before the application of EMG electrodes and taping of the fingers.

separate fingers so that the subjects could adopt a comfortable position with the elbow in a 120° angle, the wrist in line with the lower arm, and the MCP joints in a 120° angle (Fig. 1). Finger forces were measured at 100 samples/s and transmitted to a host PC running custom made software on Python version 3.4.4.1 (Python Software Foundation, Beaverton, USA). Fixing of the fingers to the force sensors allowed the measurement of both flexion and extension forces. The wrist was not constraint in order to represent natural finger use more closely.

Eight pairs of electrodes were placed on the palmar and dorsal surfaces of the right hand: 2nd lumbrical (2Lum), 3rd lumbrical (3Lum), 4th lumbrical (4Lum), abductor digiti minimi (ADM), 1st dorsal interosseous (1Do), 2nd dorsal interosseous (2Do), 3rd dorsal interosseous (3Do), 4th dorsal interosseous (4Do) (Fig. 1). After a standard skin preparation, the Ag/AgCl surface electrodes (Kendall-LTP, Chicopee, MA, USA) were placed in belly-tendon arrangement for the measurement of the intrinsic muscles. Additionally, a grid of 6 × 5 electrodes was placed on both the anterior and posterior side of the right forearm, targeting the flexor digitorum superficialis (FDS) muscle and extensor digitorum communis (ED) muscle respectively (Fig. 1). The extension grid started at the mid-point between styloid ulna and the olecranon, after which the 6 electrodes along the length of the arm were placed distal from these at a 1 cm interval. If a lack of space was present, the last electrode was placed proximal of the arm mid-point. The grid was completed by placing the other rows of electrodes towards the radial side of the posterior forearm, at 8 mm intervals. The flexion grid was placed in a similar fashion, but here the starting line was drawn between the styloid ulna and where the radius meets the elbow. The rows were placed towards the radial side of the anterior forearm, also at 8 mm intervals. The electrode placement for both intrinsic and extrinsic muscles were based on previous literature (Ejaz, Hamada, & Diedrichsen, 2015; Van Beek et al., 2016). The reference electrode was placed at the styloid ulna. All 77 electrodes were connected to an electrophysiological amplifier (Refa136, TMSi, Oldenzaal, The Netherlands). The signals were collected at a sampling rate of 2048 samples/s with a resolution of 18.39 nV per least significant bit through the system's recording software (TMSi Polybench, TMSi, Oldenzaal, The Netherlands) and stored for subsequent analysis.

2.3. Experimental protocol

The instructions and visual feedback of the different tasks were presented to the subjects on a 26 in. LCD screen. The feedback consisted of four bars, each associated with one of the fingers, filling the screen to the top when the subject applied flexion force, and to the bottom of the screen when they applied extension force. The screen was updated at a rate of 10 Hz.

First, the subjects performed maximum voluntary contraction (MVC) trials for each of the four fingers, both in flexion and extension direction. A number representing the finger to press (2 – index, 3 – middle, 4 – ring, 5 – little) was presented to the participants. After the finger indication, they were instructed to press that finger as forceful as possible against the force sensor, without moving the wrist. During the trial, the participants received online feedback of the force of all recorded fingers. The MVC trials were repeated three times for all fingers, both in flexion and extension. When wrist movement was detected by the experimenter, that specific trial was repeated.

Second, the subjects performed submaximal single finger presses. The normalized force of the instructed finger was visually presented to the participants on the screen. The participants were instructed to press 20% of force during MVC (indicated as a goal line on the screen) in the flexion direction with the indicated finger and to keep that level for 3 s. The participants completed 4 blocks, each consisting of 4 force presses of each of the fingers, resulting in 16 repetitions per finger over the course of the experiment. Each finger was repeated twice in a row (e.g. 4 4 2 2 3 3 5 5), while the order of the finger movements within a block was randomized.

2.4. Data analysis

2.4.1. Force data

Throughout the study, flexion forces were represented as positive, while extension forces were indicated as negative. Force signals were low pass filtered (10 Hz zero-phase 4th order Butterworth). MVC force was calculated as the highest value for the instructed fingers over the 3 MVC trials (Table 1). In order to calculate the enslaving effect in the subsequent 20% MVC experiments, only the active and stable data at 20% MVC force of each trial was selected. Transient periods where the absolute time derivative of force for the instructed finger was above 30% MVC/s were ignored. In addition, only data within 3 standard deviations of the mean of the force data of the instructed finger were retained (Fig. 2). This step was introduced in order to exclude data where participants had a sudden increase/decrease in force. As a result, the final analysis was done on 79 ± 3, 79 ± 4, 76 ± 10, and 77 ± 5 percent of the available data for the index, middle, ring, and little finger respectively. The enslaving effect of the non-instructed fingers was calculated as F_{norm}, the mean force produced by these fingers normalized by their earlier determined MVC force (Sanei & Keir, 2013; Slobounov et al., 2002; Zatsiorsky et al., 2000).

Table 1
MVC values for both flexion and extension measurements. Means ± SD of all 12 subjects are shown.

	Index	Middle	Ring	Little
MVC values (N)				
Flexion	17.7 ± 9.2	16.0 ± 8.5	12.2 ± 5.4	10.3 ± 4.3
Extension	5.9 ± 1.5	5.4 ± 1.7	4.2 ± 1.4	3.7 ± 1.1

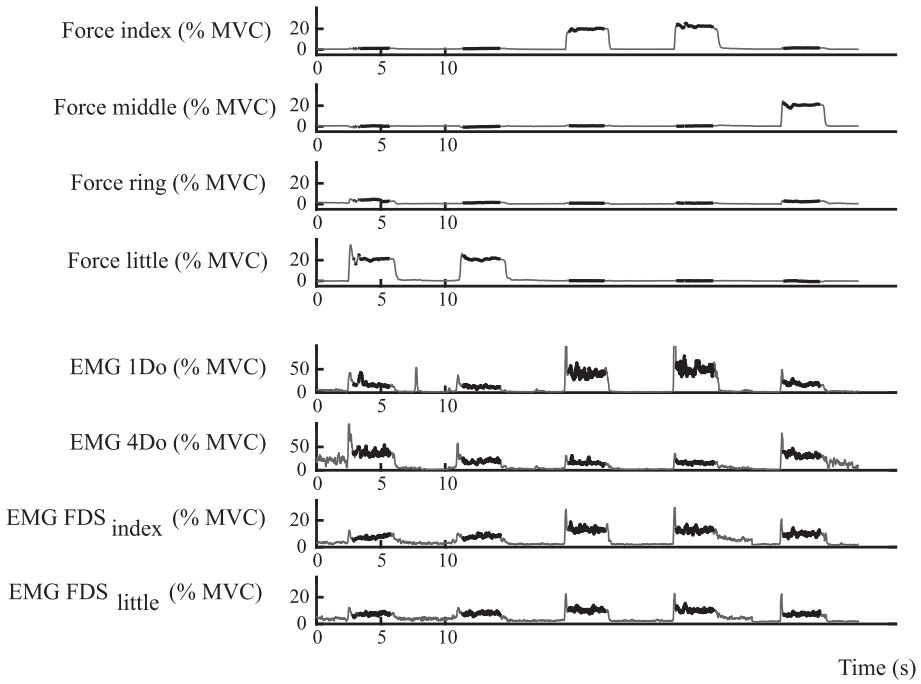

Fig. 2. Data selection. Force traces of all finger forces, and EMG traces of 4 muscles can be seen for 5 consecutive finger presses. Only data in black is retained for analysis. This selection was introduced in order to exclude data that was not representative of an isometric 20% MVC press, e.g. the overshooting of the little finger target at the beginning of the first trial. This also assured that non-representative peaks were not included in the EMG analysis.

2.4.2. EMG data

EMG signals were analysed as belly-tendon pairs for the intrinsic muscles and as bipolar derivations between nearest neighbours along the length of the arm for the electrode grids. The latter resulted in a 5 × 5 bipolar electrode grid both for the flexion and for the extension side of the forearm. The advantage of the bipolar derivation with a small (1 cm) interelectrode distance is that it leads to a reduction in cross-talk (Roeleveld, Stegeman, Vingerhoets, & Oosterom, 1997). All EMG signals were mean corrected, and bandpass filtered (zero-phase 4th order Butterworth) between 10 and 500 Hz. The root mean square (RMS) of the signal was determined with a sliding window of 100 ms, after which the signal was resampled to 100 Hz to match the force signals (Fig. 2). The resting value, defined as the lowest mean RMS over a 1 s window over all trials, was subtracted from each channel, and the data was cleaned from obvious outliers due to loss of proper EMG-skin connection. All data was normalized by dividing each channel by the maximum activity on that channel during the MVC trials (EMG_{norm}). The neural activation in EMG channels during each finger presses was calculated as the mean EMG_{norm} for that trial during the same active and stable duration calculated for the forces (Fig. 2).

In order to perform the activation analysis on the extrinsic muscles, each finger movement was associated with a single electrode pair placed on the extrinsic muscles in both flexion and extension. The method used to select the extrinsic channels was based on Van Beek et al. (2016). In brief, for each finger, the channel with the highest cross-covariance to the F_{norm} of that finger was selected. Cross-covariance partly relies on the EMG amplitude of the channel. However, the selected channel was not necessarily the channel with the highest EMG amplitude for that finger, as it also depends on the correlation with the force profile. The channel selection was determined based on the MVC trials, as these consisted of both flexion and extension finger presses and were independent of the single finger trials of the actual analysis. In order to select channels associated with flexion movements, only the channels on the ventral side of the arm were considered, while only these on the dorsal side were taken into account for the extension selection. The selection algorithm determined the channels with the highest cross-covariance between EMG_{norm} and the F_{norm} for each finger. In some cases, an extrinsic channel was selected for more than one finger. In this case, the highest unique channel was selected instead. For the flexion channels, the channel with the highest cross-covariance could be selected as representative for that finger in 63% of the cases (rank 1), the mean rank was 1.71, and the highest selected rank was 4. For the extension channels, 58% of the selected channels had rank 1, the mean rank was 1.75, and the highest rank considered in the results was 5. Channel selection results showed no significant differences over instructed fingers for flexion ($p = 0.86$) and extension ($p = 0.44$), or between flexion and extension ($p = 0.85$). The location of the selected electrodes for flexion and extension of the four fingers for all participants can be seen in Fig. 3. After this selection of extrinsic channels, further analysis was done on 16 EMG channels: 8 intrinsic (4 flexion, 4 extensions), and 8 extrinsic (4 flexion, 4 extension) channels. The extrinsic channels were named based on the finger activation they were associated with, namely: FDS_{index}, FDS_{middle}, FDS_{ring}, FDS_{little}, ED_{index}, ED_{middle}, ED_{ring}, and ED_{little}.

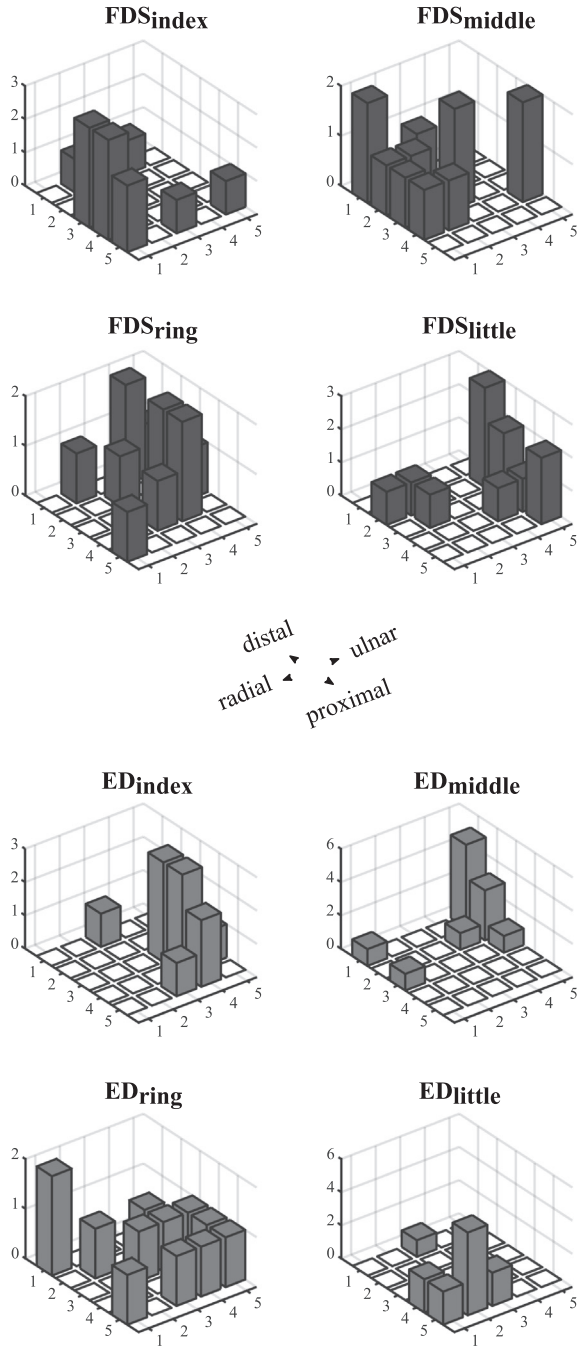

Fig. 3. Cumulative representation of the FDS and ED muscle positions over the different participants. The grid represents the 5 × 5 bipolar electrodes. Flexor muscles (agonist in the flexion task) are shown in a darker grey than the extensor muscles (antagonist in the task).

2.4.3. Statistics

Normality of the data was tested through the Shapiro-Wilk test. When the null-hypothesis of normality could not be rejected, a one-way ANOVA was performed. When ANOVA showed significance, post hoc analysis was performed with a *t*-test using Bonferroni correction. In multiple cases, the Shapiro-Wilk test revealed that the data was not normally distributed. As a result, the independent samples Kruskal-Wallis test was used in order to determine whether there were differences between either muscle activations or finger forces. When the test revealed a significant difference, further post hoc analysis was done using a pairwise Kruskal-Wallis comparison with Bonferroni correction. The significance level was set at 0.05 in all cases.

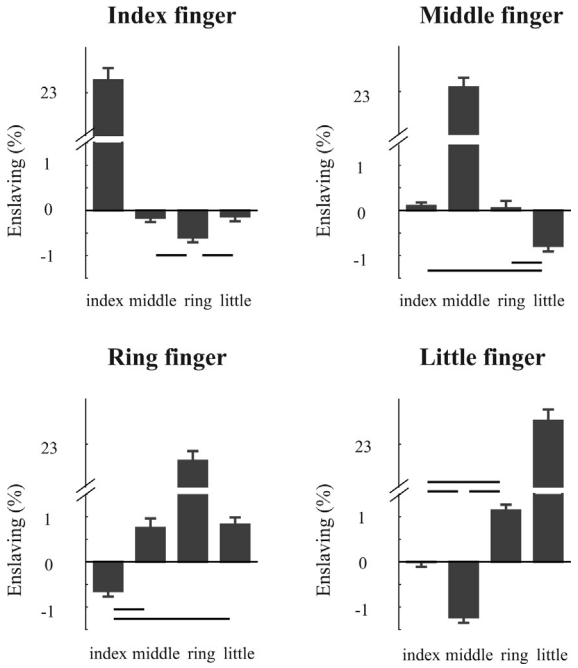

Fig. 4. Force enslaving of the different non-instructed fingers. Negative values for enslaving indicate extension forces. The horizontal lines indicate significant differences in exerted force between the three non-instructed fingers ($p < 0.05$).

3. Results

3.1. Force enslaving

The Shapiro-Wilk test indicated that the force data was not normally distributed ($p < 0.001$). For each instructed finger, the Kruskal-Wallis test was used to determine if the forces of the different non-instructed fingers resulted from the same distribution. This test assumes that the forces of the different non-instructed fingers are independent. This assumption holds when considering that, while the forces of the instructed finger determines the enslaving, the force levels of the non-instructed fingers were small and therefore had no influence on each other (Kilbreath et al., 2002). The tests showed that the enslaving forces of the different non-instructed fingers were significantly different from one another ($p < 0.001$ for all instructed fingers). The post hoc pairwise Kruskal-Wallis comparisons are documented in Fig. 4. The results of the post hoc analysis of the forces of the non-instructed fingers when the index finger was instructed was distinct from that when the other fingers were instructed. Here, the adjacent middle finger was not different from the little finger ($p = 1$), while the ring finger was significantly different from both ($p < 0.001$ in both cases). With the middle finger as instructed finger, the adjacent fingers have a significantly higher level of enslaving than the little finger ($p < 0.001$ for both the index – little, and ring – little comparison), while there was no difference between the two adjacent fingers of that finger ($p = 0.076$). The same can be seen when the ring finger was the instructed finger: comparisons index – middle, and index – little finger both have a p-value < 0.001, while middle – little finger showed no significance ($p = 1$). In the case of the little finger as instructed finger, all pairwise combinations were significant (all $p < 0.001$).

3.2. Muscle activation

Since RMS rectifies the almost normally distributed EMG signals, the estimation of EMG amplitude through RMS leads obviously to not normally distributed data. The Shapiro-Wilk test confirmed this ($p < 0.001$). The activation of the intrinsic muscles was more distinctly corresponding to the instructed finger than the activation of the extrinsic muscles (Fig. 5). However, per instructed finger, the Kruskal-Wallis test showed significant differences in EMG amplitude between the investigated muscles for both intrinsic and extrinsic muscles ($p < 0.001$ in all cases).

As most pairwise comparisons with Bonferroni correction were significant in the post hoc analysis for the intrinsic muscles (Fig. 5), we focused on the non-significant couples. These included the muscles that are anatomically located on both sides of the active fingers: 1Do vs 2Do when the index finger was instructed ($p = 1$), 2Lum vs 3Lum and 2Do vs 3Do when the middle finger was instructed ($p = 0.051$, and $p = 1$ respectively), 3Lum vs 4Lum and 3Do vs 4Do when the ring finger was instructed ($p = 1$ in both cases), and 4Lum vs ADM when the little finger was instructed ($p = 1$). These muscles were significantly more active than the muscles not anatomically located around the instructed finger, except for the single case of 2Lum vs 4Lum when the middle finger was instructed ($p = 0.57$).

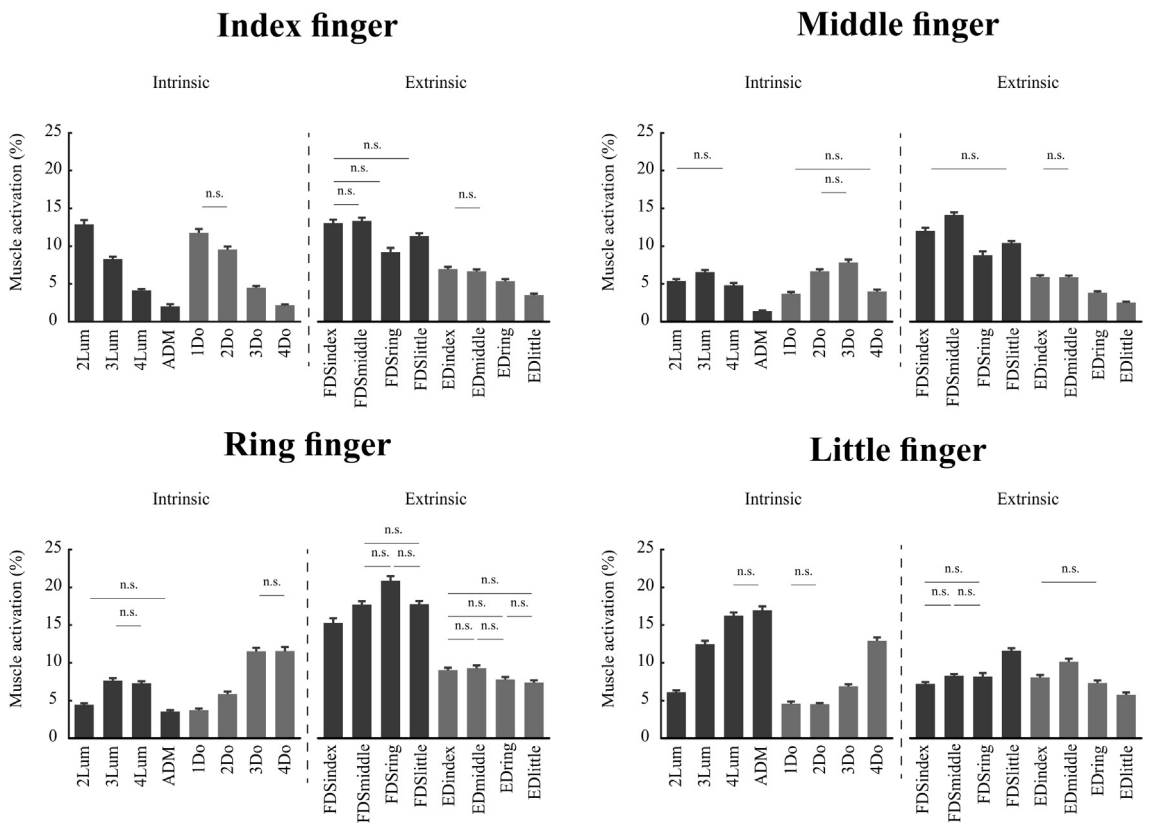

Fig. 5. Muscle activations per instructed finger for the different muscles. Flexor muscles (agonist in our flexion task) are shown in a darker grey than the extensor muscles (antagonist in the task). A dashed line separates the investigated intrinsic and extrinsic muscles. Non-significant pairwise comparisons of muscle activation are indicated in the figure, as most comparisons were significantly different ($p < 0.05$). Pairwise comparisons are made within muscles with the same location (intrinsic–extrinsic), and function (agonist–antagonist).

When considering the extrinsic muscles, separate patterns emerged for the agonistic and antagonistic muscle channels. When the middle and little finger were instructed, FDS channels associated with the instructed finger (FDS_{middle}, and FDS_{little}, respectively) were significantly higher than the others. This phenomenon did not reach significance when the ring finger was instructed, and even disappeared when the index finger was instructed. The EMG amplitudes of the ED channels did hardly differ when the different fingers were instructed, and the ED channels associated with the extension movement of the instructed finger were not highest when that same finger performed a flexion movement.

Looking at the differences in activation for one muscle when the different fingers are active allows us to investigate whether the force enslaving pattern is reflected in the activation of the muscles. The way in which EMG activity of the muscles was modulated for the different instructed fingers affirmed the distinction between intrinsic and extrinsic muscles. In all cases, Kruskal-Wallis analysis showed the presence of significant differences between the activation level when different fingers were instructed, which allowed for post hoc analysis (Fig. 6). For the intrinsic muscles, most muscles were significantly more active when the fingers that are anatomical neighbours were instructed (Fig. 6, upper two rows). For example, 2Do is more active when the index and middle finger are instructed, and 4Do when the ring and little finger are activated. The exceptions to this case were 2Lum for the activation of the middle finger, 3Lum for the activation of both the middle and ring finger, and 3Do for the activation of the middle finger. The extrinsic muscles on the other hand, seemed to be modulated in response to finger pressing, regardless of the finger they were associated with (Fig. 6, lower two rows). In all but 1 case, the muscles were most active when the ring finger was instructed. The exception is the ED_{middle} muscle. In three other cases, the ring finger movement did not lead to a significant muscle activity increase in specific post hoc comparisons: for FDS_{index} (in index vs ring finger movement: $p = 0.53$), ED_{index} muscle (in ring vs little finger movement: $p = 0.21$), and EDring muscle (in ring vs little finger movement: $p = 1$).

4. Discussion

While there is an extensive literature on finger enslaving, this is to our knowledge the first report that investigated the simultaneous activity of both intrinsic and extrinsic hand muscles during single finger pressing. The main results are (1) a distinct neural drive to intrinsic and extrinsic muscles; (2) modulation of the agonistic and antagonistic intrinsic muscles based on the instructed finger; (3) a broad activation in the extrinsic muscles, with task-specific modulation for the agonistic extrinsic muscles.

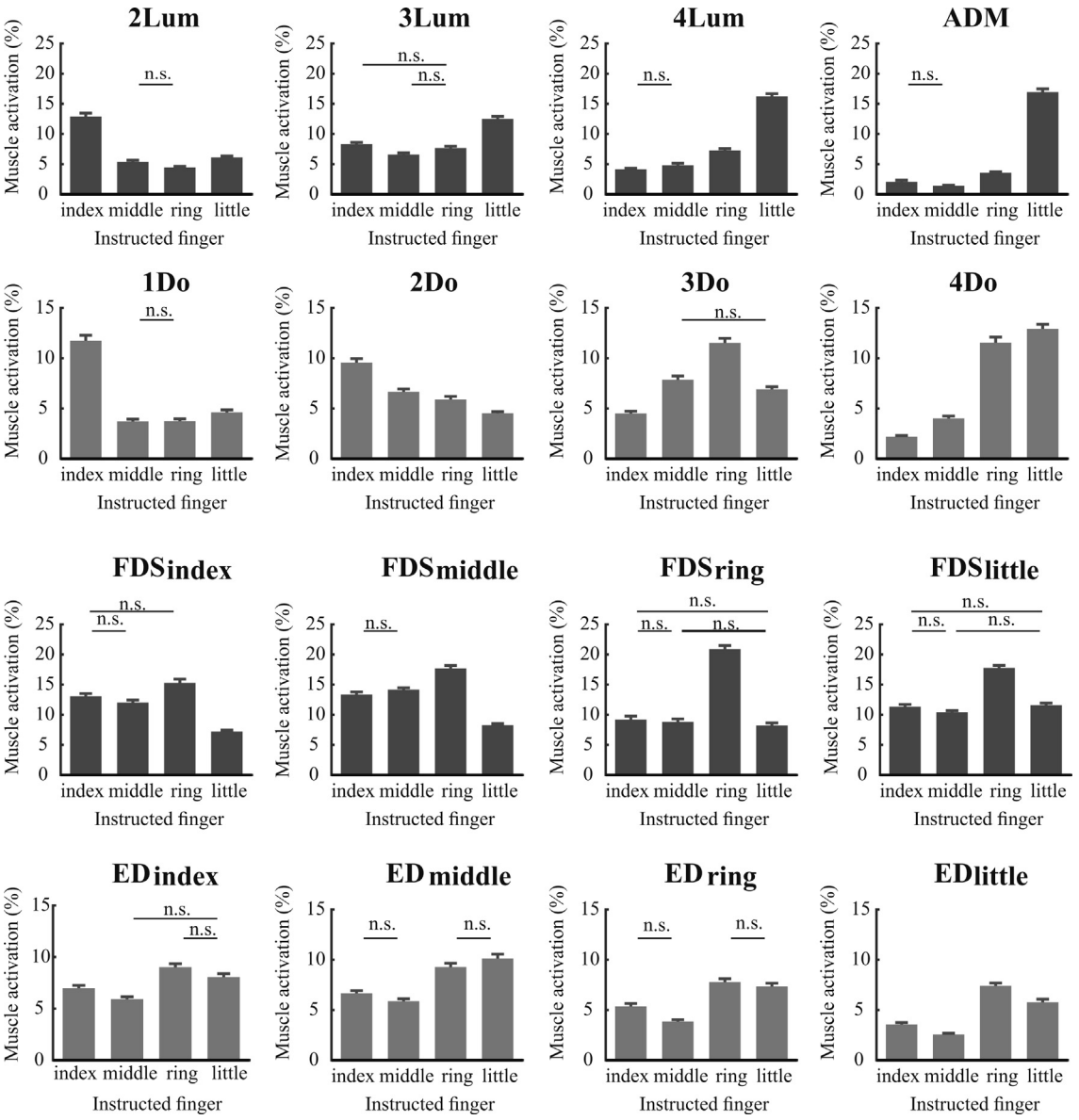

Fig. 6. Differences in the activation of muscles when different fingers were instructed. Flexor muscles (agonist in our flexion task) are shown in a darker grey than the extensor muscles (antagonist in the task). Non-significant pairwise comparisons of muscle activation between instructed fingers are indicated in the figure, as most comparisons were significantly different ($p < 0.05$).

The analysis of muscle activation in the intrinsic muscles showed a clear relationship between the EMG amplitude and the instructed finger (Fig. 5). The emergence of this pattern in agonistic muscles can be related to the task. The concurrent presence of this pattern in the antagonistic muscles is related to the stabilization of the fingers required during constant force production (Li et al., 2000; Valero-Cuevas, 2005; Valero-Cuevas et al., 2007). The fact that the intrinsic muscles were active during force exertion of both neighbouring fingers (Fig. 6) can be well explained by their anatomy. The lumbrical muscles originate from the distal tendons of the flexor digitorum profundus. The second lumbrical is unipennate, while the third and fourth are bipennate originating from the tendons corresponding to the middle and ring, and ring and little finger respectively (Wang, McGlinn, & Chung, 2014). The dorsal interosseous muscles on the other hand are all bipennate (Liss, 2012).

Surface EMG allows that an electrode picks up information from muscles other than the intended muscle due to volume conduction (De Luca & Merletti, 1988). In this study, bipolar derivation of the signals was used, reducing the amount of such cross-talk from unintended muscles (Roeleveld et al., 1997). The size of the targeted intrinsic muscles, together with the fact that they are located superficially, decreases the likelihood of cross-talk (Roeleveld et al., 1997). However, if cross-talk was present, it would mean that the level of individuation of the intrinsic fingers is even higher than reported here.

The activation patterns of the extrinsic muscles were distinct from those of the intrinsic muscles (Fig. 5). The agonistic muscle

pattern followed that of a previous surface EMG study where the EMG amplitude of the electrode associated with a certain movement was generally higher than that of the electrodes associated with the non-instructed fingers (Van Beek et al., 2016). However, in both that study and the present one this was not always significant, which suggests that there is an overall activation in the extrinsic agonistic muscles that is not associated with fine finger movements. This overall activation might well be due to the necessity to stabilize the wrist through muscle activation (Mirakhorlo, Maas, & Veeger, 2017, in press) as there was no wrist splint used in this study, contrary to most enslaving studies (Sanei & Keir, 2013; Zatsiorsky et al., 1998, 2000). Recent work by May and Keir (2018) shows that activity of the anatomically determined FDS_{index} compartment was not the highest when the index finger was active while the wrist was splinted in their experiment. This suggests that the extrinsic agonistic muscle pattern found in this paper is not fully method-dependent. The antagonistic muscle pattern of our study did not follow the previously published surface EMG study (Van Beek et al., 2016). There, the electrode associated with the instructed finger was less active than the ED regions associated with the non-instructed fingers. While the reduction in activation of the antagonistic muscle was necessary to perform the free finger flexion movement in the study of Van Beek et al. (2016), an activation of antagonistic muscle activity was necessary in this study in order to stabilize the wrist and fingers during the force pressing task. Previous studies showed that extrinsic muscles are the main source of force in single finger tasks, with up to 80% of force resulting from extrinsic muscles when the force is applied at the distal phalanx (Li et al., 2001; Milner & Dhaliwal, 2002). The discrepancy in the results of extrinsic muscle patterns in the literature highlights the need to thoroughly consider the experimental setup when studying finger enslaving and neural control of fine hand movements. Setups where the wrist is splinted are not capable of mimicking single finger forces and EMG patterns, as freely performed finger movements naturally occurring require a concurrent control of the wrist. The plane in which the fingers operate also varies between studies, with an almost even split between studies where the fingers produce motions in a horizontal (May & Keir, 2018; Sanei & Keir, 2013; Van Beek et al., 2016), or vertical plane (Li, Latash, & Zatsiorsky, 1998; Quaine, Paclet, Letué, & Moutet, 2012; Slobounov et al., 2002; Zatsiorsky et al., 1998, 2000). Positioning fingers to act in a horizontal plane eliminates gravitational effects when studying flexion and extension of the fingers, although these effects might also be negligible in the vertical plane when compared to the force levels present in enslaving studies (commonly between 20% MVC and 100% MVC).

Previous research has shown that cross-talk in the forearm is less for muscles associated with finger than with wrist movement (Kong, Hallbeck, & Jung, 2010), and that inter-electrode distances of 2 cm reduce cross-talk to 10–20% of the original signal (Lowery, Stoykov, Dewald, & Kuiken, 2004; Roeleveld et al., 1997). The channel selection algorithm resulted in a mean distance of 2.58 ± 1.03 cm for flexor electrodes and 2.80 ± 1.13 cm for the extension electrodes. These results, together with the fact that the muscles had a similar pattern for the fingers that were located nearby, and those farther away, suggest that the activation pattern of the extrinsic muscles is mainly determined by the targeted muscle bellies of FDS and ED.

The force enslaving results (Fig. 4) confirmed the results of other studies in which the fingers adjacent to the instructed finger showed the highest level of enslaving (Kilbreath et al., 2002; Sanei & Keir, 2013; Schieber, 1991; Slobounov et al., 2002; Van Den Noort et al., 2016; Zatsiorsky et al., 2000). The values found for the enslaving were in the same order of these found by Sanei and Keir (2013), while they were lower than in the study of Slobounov et al. (2002). This discrepancy might be explained by the task execution. The fingers of the participants in the current experiment were fixed to the force sensors and, therefore, restricted in both flexion and extension movements, while the fingers of the participants in the study of Slobounov et al. (2002) rested on top of force sensors without any extension restrictions. As a result, it is noteworthy that all non-instructed fingers also exhibited extension forces during some trials of the experiment, which only consisted of flexion forces for the instructed fingers (Fig. 4). Overall, fingers adjacent to the instructed finger exhibited flexion enslaving forces. However, non-neighbouring fingers commonly showed extension forces, possibly due to the rotational forces on the wrist (Li et al., 1998; Quaine et al., 2012). Extension forces were also found in the study of Sanei and Keir (2013), although to a lower extent as they fixed the wrist during the experiment. Experiments where the fingers are only restricted in flexion direction would not be able to pick up on these rotational forces. The many different enslaving results throughout these studies show that enslaving is dependent on the exact task and the experimental constraints.

The force enslaving pattern was visible in the intrinsic muscles (Fig. 6). The lumbrical muscles also show some activation when they do not insert on the instructed finger. However, this activation is not necessarily the cause of enslaving forces, as the lumbrical muscles also control the extension of PIP and DIP joints, and therefore play a role in the stabilization of the finger (Valero-Cuevas, 2005; Valero-Cuevas et al., 1998). The same pattern resembling enslaving was not reflected in the EMG amplitude pattern of the extrinsic agonistic muscles. For example: we expected to see that FDS_{index} would be most active during index flexion presses, followed by the task for which it is adjacent, middle finger pressing. However, as can be seen in Fig. 6, FDS_{index} is most active during ring finger flexion, and has similar activation for both index and middle finger flexion. This pattern, where FDS activation is highest for ring finger flexion, can be seen in all muscles. The selection criteria of extrinsic EMG channels, where the channel selected did not necessarily have the highest activation, but was highly correlated to the force pattern, might have influenced this result. However, Fig. 5 shows that there is a finger-specific modulation in the extrinsic flexor muscles, and that the ring finger requires an overall higher activation. This indicates that the electrodes were selected correctly, but that the overall level of activation of all extrinsic muscles depends on which finger is active. This might suggest that force enslaving is a result of the inability of the intrinsic muscles to counteract the broad activation in the extrinsic muscles.

The method selecting the extrinsic channels representative for specific movements was adapted from Van Beek et al. (2016). By selecting channels for both flexion and extension that correlated most with the respective finger force presses, this method allowed to take the complex and individuated anatomy of the FDS and the ED into account. While muscles selected for some finger force tasks – such as the flexion of the little finger, and extension of index, middle, and little finger – are located similarly over different participants, others are distributed over different areas (Fig. 3). This is in accordance with the previous study of Van Beek et al. (2016). The location of the flexor electrodes generally matched that found in previous studies (Bickerton, Agur, & Ashby, 1997; Henzel et al.,

2010; Van Beek et al., 2016), while the channels selected for the extensor forces did not follow previously found placement (Leijnse, Campbell-Kyureghyan, Spektor, & Quesada, 2008; Van Beek et al., 2016). This difference may be due to a difference in the intensity of the tasks studied as both other studies employed finger movement at a low intensity (either tapping on a table or extension movements), while the channels for this study were selected on the basis of 100%MVC extension force tasks. However, they mainly highlight the individual nature of forearm musculature (Maas, Veeger, Dirkjan, & Stegeman, 2018; Van Beek et al., 2016). These results suggest that caution should be applied when determining extrinsic muscle bellies by anatomical landmarks and palpation. Rather, using a higher number of electrodes, in the form of grids, to later determine the best candidates is warranted.

5. Conclusion

In conclusion, the present study shows distinct muscle patterns in intrinsic and extrinsic hand muscles during single finger isometric force pressing. While intrinsic muscles exhibit individuation, extrinsic muscles reveal a broad activation, largely independent of which finger was instructed to press, with some finger-dependent modulation on top. Stabilisation of the finger and wrist joints appears to determine the co-activation of agonistic and antagonistic muscles in both intrinsic and extrinsic muscles. The broad activation in extrinsic agonistic muscles, presumed to stabilize the wrist, was also found in the extrinsic antagonistic muscles, while the task-dependent modulation was only visible in the agonistic muscles. The task-specific intrinsic muscles showed clear modulation based on the instructed finger, where the patterns in agonistic and antagonistic muscles are similar, seemingly in order to reach finger joint stabilization. Our results indicate that the finger specific activation of intrinsic muscles is not sufficient to fully counteract finger force enslaving caused by a broad activation of the extrinsic muscles.

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Conflict of interest

The authors declare that they have no conflict of interest of financial ties to disclose.

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